

LARVAE AND PUPAE OF *CENTRONOPUS CALCARATUS* AND
CENTRONOPUS SUPPRESSUS (COLEOPTERA: TENEBRIONIDAE),
WITH AN ESSAY ON WING DEVELOPMENT IN PUPAE

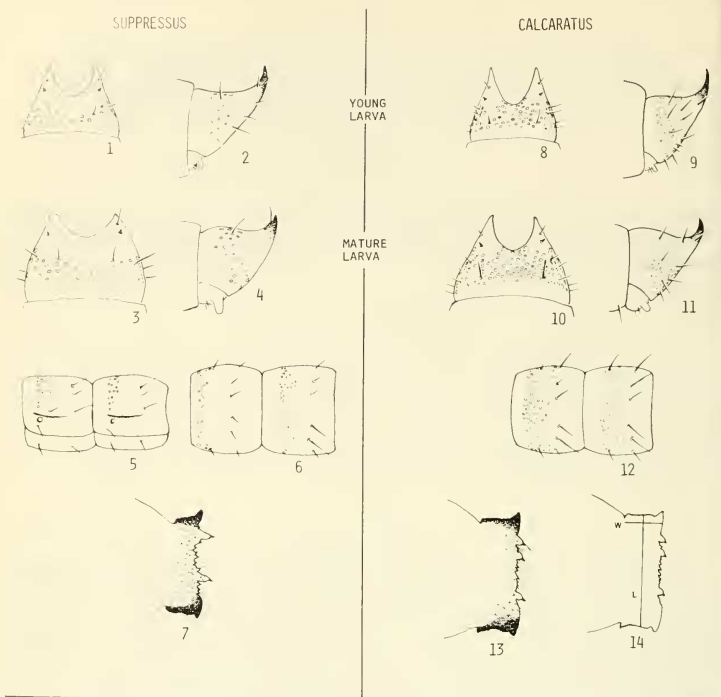
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Abstract.—The larvae and pupae of *Centronopus calcaratus* (Fabricius) from eastern United States and Canada and *C. suppressus* (Say) from Mexico are described and illustrated, and a determination key is provided. Adult wing length and pupal wing sheath length are studied and correlated. A short pupal wing sheath in a species indicates widespread winglessness in adults of the higher taxon.

The genus *Centronopus* Solier, a member of the Tenebrionini, contains 10 species, all found in the Western Hemisphere under bark of logs. I reviewed the species recently (1962:1-19) but, except for a few host records of larvae, discussed only adults. Prior to my review the genus was usually known by the generic name *Scotobates*. Until now only the species *C. calcaratus* (Fabricius), from the eastern United States and Canada, was known in the larval and pupal stages. St. George (1924:11) included *Centronopus* (= *Scotobates*) based only on *calcaratus*, in his key to the North American larvae of the Tenebrionini, then called Tenebrioninae; he illustrated (Figs. 45-48) the hypopharyngeal sclerome, the prothoracic and mesothoracic legs, and the apex of the abdomen of *C. calcaratus*. Craighead (1950:217) included the genus, based on *C. calcaratus*, in a key to the larvae of the more common wood- and fungus-infesting Tenebrionidae in the eastern United States; he presented (Fig. 45D) a lateral view photograph of the larva. Daggy (1947:259) included *Centronopus* (= *Scotobates*) *calcaratus* in his key to the pupae of the Tenebrionidae of Indiana, illustrating (Pl. 3, Fig. 13) a lateral abdominal process.

The immature stages of another species, *Centronopus suppressus* (Say), have come to light. In the Museum of Comparative Zoology this species is represented by two larvae, two pupae, and two adults, collected together under bark of *Pinus* sp., 10 miles south of Las Vigas, Veracruz, Mexico.



Figs. 1-6. *Centronopus suppressus*, larva. 1. Apex of abdomen of young larva, dorsal view. 2. Same, lateral view. 3. Apex of abdomen of mature larva, dorsal view. 4. Same, lateral view. 5. Second and third abdominal segments, lateral view. 6. Same, dorsal view. Fig. 7. *Centronopus suppressus*, pupa, third lateral abdominal process, dorsal view.

Figs. 8-12. *Centronopus calcaratus*, larva. 8. Apex of abdomen of young larva, dorsal view. 9. Same, lateral view. 10. Apex of abdomen of mature larva, dorsal view. 11. Same, lateral view. 12. Second and third abdominal segments, dorsal view. Figs. 13-14. *Centronopus calcaratus*, pupa. 13. Third lateral abdominal process, dorsal view. 14. Same, diagram for measurements. W—width. L—length.

at 10,000 feet, on 15 July 1971, by A. Newton. The adults were determined by me; the larvae and pupae were easily determined to belong to *Centronopus* by using the keys mentioned and were then assumed to be *C. suppressus* because of their association with the adults. (The following Mexican localities, from specimens in the Ohio State University Collection, can be added to the known distribution of *C. suppressus*: Puebla: Xometla, 1 mi

E of Chalchicomula, 8000 ft, pineland, base of Orizaba, Veracruz: 11 mi NE of Perote, pineland at 7000 ft; 11 mi N of Perote, 8000 ft; 2-3 mi W of Acultzingo, 7000 ft; 1 mi N of Fortin, in banana grove; Jalapa. The following are in the California Insect Survey Collection at Berkeley: Veracruz: 15 mi W of Jalapa, 7600 ft; 8 km SE of Las Vigas, 2200 m, under bark *Pinus*; 5 km SW of Las Vigas, 2440 m, ex *Quercus* stumps; 5 mi SE of Las Vigas, 7500 ft; 18 km SE of Las Vigas, 2200 m, under bark *Quercus*.)

According to my classification of adults (1962), the genus is composed of two subgenera, *Centronopus* (including *C. suppressus*) and *Menechides* Motschulsky (including *C. calcaratus*). Until larvae and pupae of additional species are described, it is impossible to determine if differences are of subgeneric or only of specific rank. At present these characteristics can be used only to differentiate species, not to classify.

KEY TO LARVAE OF *CENTRONOPUS*

- Anterior abdominal terga with coarse punctures dense on anterior $\frac{1}{3}$ but sparse or absent on posterior $\frac{2}{3}$ (Fig. 6). Seta present dorso-posteriorly to spiracle and dorsal to lateral line on abdominal segments 1-2 but absent on segments 3-8 (Fig. 5) *suppressus* (Say)
- Anterior abdominal terga with coarse punctures dense on anterior $\frac{2}{3}$ (Fig. 12). Seta present dorsoposteriorly to spiracle and dorsal to lateral line on abdominal segments 1-8 *calcaratus* (Fabricius)

The presence of two large, simple, sharp urogomphi and many coarse punctures on the 9th abdominal tergum are characteristic for *Centronopus*. The size of these urogomphi varies both ontogenetically and interspecifically in the genus. In both species the urogomphi are relatively slenderer and longer in younger instars than in older instars (Figs. 1-4, 8-11). The interspecific differences, given below, are not used in the determination key because of ontogenetic variation.

Larvae of this genus do not have on the thoracic and abdominal terga the transverse anterior sulcus that is present on many tenebrionid larvae; this sulcus is usually sharply margined anteriorly but not margined posteriorly. Nevertheless, the meso- and metathoracic terga and anterior abdominal terga have a weak transverse depression; the coarse punctures are usually denser in the depression than on the remainder of the tergum.

Larvae of *C. suppressus*.—Prothoracic tergum without coarse punctures; meso- and metathoracic terga and anterior abdominal terga with coarse punctures dense on anterior $\frac{1}{3}$ but sparse or absent on posterior $\frac{2}{3}$ (Fig. 6), then coarse punctures becoming denser on posterior $\frac{2}{3}$ on posterior terga until quite dense on terga 6-8; tergum 9 with coarse punctures dense on base, very sparse between urogomphi, and absent on urogomphi (Figs. 1-4). Punctures finer and pigmentation surrounding punctures less extensive

than in *C. calcaratus*. Dorsoposteriorly to each spiracle and dorsal to lateral line a seta is present on abdominal segments 1–2 but absent on segments 3–8 (Fig. 5). Urogomphi (Figs. 1–4) stouter and shorter than in a comparable instar in *C. calcaratus*; each urogomphus with a few transverse wrinkles accompanying setiferous punctures.

Larva of *C. calcaratus*.—Thoracic and abdominal terga with coarse punctures dense on anterior $\frac{2}{3}$ (Fig. 12); punctures slightly denser on anterior $\frac{1}{3}$ on all but prothoracic and 9th abdominal terga; punctures unevenly distributed on posterior area, leaving a few bare spots; tergum 9 with coarse punctures dense on entire surface and extending onto bases of urogomphi. Punctures coarser and pigmentation surrounding punctures more extensive than in *C. suppressus*. Dorsoposteriorly to each spiracle and dorsal to lateral line a seta is present on abdominal segments 1–8. Urogomphi (Figs. 8–11) slenderer and longer than in a comparable instar in *C. suppressus*; each urogomphus smooth except for punctures.

KEY TO PUPAE OF *CENTRONOPUS*

- Lateral abdominal process excurved on medial area of posterior border (Fig. 7); processes relatively narrow, for example, width of 3rd process 27% of length; posterior border of pronotum incurved
 *suppressus* (Say)
- Lateral abdominal process incurved on medial area of posterior border (Fig. 13); process relatively broad, for example, width of 3rd process 34% of length; posterior border of pronotum bisinuate
 *calcaratus* (Fabricius)

Measurements of the lateral abdominal processes are made as follows (Fig. 14): Width is measured along an imaginary line (W), perpendicular to the longitudinal axis of body, from medial end of sclerotized anterior edge of process to lateral edge; length is measured along imaginary line (L), parallel to longitudinal axis of body, at middle of width (W), from anterior edge of process to posterior edge.

The key is adequate for separation of species; formal descriptions are not given. The size, number, and distribution of tubercles on lateral abdominal processes (Figs. 7, 13) are variable and should not be used for identification.

In *Centronopus*, as in other insects with exarate pupae, many adult characteristics of shape can be seen on the pupa—I do not mean here the adult which can often be seen inside of and through the pupal skin—but small details like punctuation, setation, color, and even larger features that might be distorted by pupal habitus cannot usually be seen on the pupa. In the two species under consideration the small specific adult differences cannot be seen in the pupae, but two of the four subgeneric differences are apparent. The adults of *Centronopus* are grouped into two subgenera by the

following: *Centronopus* (with *C. suppressus*): 1—posterior pronotal border incurved, 2—metathoracic wings short and spatulate, hereafter called brachypterous, 3—metasternum short, 4—elytra narrow at base and humeri rounded; *Menechides* (with *C. calcaratus*): 1—posterior pronotal border bisinuate, 2—metathoracic wings long and broad, hereafter called winged, 3—metasternum long, 4—elytra broad at base and humeri subangulate. (Incidentally, the last three characteristics could actually be considered as one because they usually occur together in brachypterous and wingless Tenebrionidae and many other Coleoptera. Though the elytra must be lifted if one is to be certain of the presence of wings, a prediction of brachyptery or winglessness usually can be made on the basis of length of metasternum and width of elytral base.) As to the presence of subgeneric structures in these pupae, the first and third can be seen on the pupa, the fourth cannot be seen on the pupa because the mesothoracic wing sheaths are quite narrow and curved around the side of the body, and the second can be seen in part on the pupa. This last mentioned, the condition of the mesothoracic wing sheaths of the pupae, is discussed in the following essay.

WING DEVELOPMENT IN PUPAE

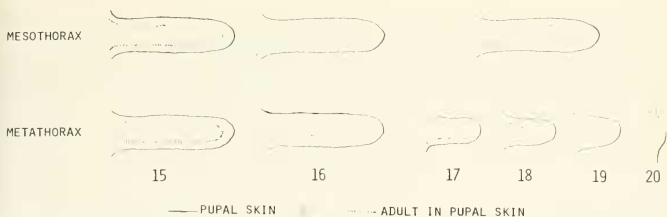
Beetles with long elytra and long wings have in their pupal stage long elytral sheaths and long wing sheaths. The long elytra and wings of the adult fill the cavities of the pupal sheaths. That is the condition in the pupa of *Centronopus* (*Menechides*) *calcaratus*, a fully winged species. On the other hand, in the pupa of *Centronopus* (*Centronopus*) *suppressus*, a brachypterous species, the wing sheath is long, even though the short spatulate adult wing fills only a small part of the wing sheath. It would seem, at first glance, that a short pupal wing sheath would have developed.

In an excellent study on the structure and development of flightless Coleoptera by Smith (1964) and an earlier study on rudimentary wings by Waddington (1942) the morphological description of the development of various conditions of wings in the Ptinidae helps toward an understanding of the wings of *Centronopus*. From Smith it can be inferred that in the Ptinidae the condition of adult wing development [completely formed, reduced (brachypterous), or absent] proceeds in five different ways by the development in the larva of the imaginal discs and/or by the development in the pupa of the adult wing within the wing sheath. (1) In a fully winged species the wing develops from a fully-developed imaginal disc, becomes a large wing in a large pupal wing sheath, and develops normally in that sheath. (2) In a brachypterous species the wing develops from a large imaginal disc, becomes a large wing in a large pupal wing sheath, and finally degenerates to less than full size in the sheath; or (3) in a brachypterous species the wing develops from a small imaginal disc, becomes a small wing

in a small pupal wing sheath, and degenerates to an even smaller wing in the sheath. (4) In a completely wingless species the wing develops from a tiny imaginal disc, becomes a tiny wing in a very small pupal wing sheath, and degenerates completely in the sheath; or (5) in a wingless species the wing is absent in the pupa because of the absence of an imaginal disc in the larva and the pupal wing sheath is absent. Undoubtedly the condition of the adult wing and pupal wing sheath in *Centronopus calcaratus* corresponds to the first condition described by Smith in the Ptinidae and that of *Centronopus suppressus* to the second condition.

My observation of pupal wing sheaths of *Centronopus* and the article by Smith led me to wonder about the pupae of other wingless or brachypterous tenebrionids. In beetles with fully-developed elytra and wings, the wing sheath is as long as the elytral sheath, so I have given the length of the pupal wing sheath as compared with the length of the elytral sheath. *Meracantha contracta* (Palisot) (Meracanthini) has the pupal wing sheath similar in length, shape, and thickness to the elytral sheath; and the adult wing is very short and spatulate. *Eleodes* sp. (Eleodini), *Blaps polychresta* (Forskål) (Blaptini), and *Zopherus nodulosus haldemani* Horn (Zopherini) have pupal wing sheaths approximately two-thirds the length of, narrower than, and much thinner than the elytral sheaths; species of *Eleodes* and the other two known species have adult wings that are very short and spatulate. *Asidopsis* sp. (Asidini) has the pupal wing sheath approximately one-third the length of, as broad as, and much thinner than the elytral sheath; and the adult wing is absent in the genus. To be sure, the sample studied is very small for a family the size of the Tenebrionidae; the reason, of course, is that pupae of beetles are seldom collected and preserved.

Wing sheaths of pupae of other families of beetles that were examined were measured in the same way. The following data represent five types of pupal wing sheaths and adult wings; the numbering system is not comparable to that given in my discussion of Smith's findings. 1—The pupal wing sheath is long, and the adult wing is spatulate (Fig. 16): Curculionidae: *Trachyphloeus* sp. (Otiiorhynchinae, Trachyphloeini), *Nemocestes* sp. (Otiiorhynchinae, Peritelini), *Graphognathus* sp. (Brachyderinae, Naupactini), *Epicaerus aurifer* Boheman (Brachyderinae, Barynotini), *Calomycterus setarius* Roelofs (Eremninae, Cyphicerini), *Dyslobus alepidotus* Ting (Leptopiinae, Leptopiini); Carabidae: *Carabus nemoralis* Müller (Carabinae, Carabini). 2—The pupal wing sheath is short, and the adult wing is short (Fig. 17): Curculionidae: *Otiiorhynchus sulcatus* (F.) and *O. ovatus* (L.) (Otiiorhynchinae, Otiiorhynchini). 3—The pupal wing sheath is short, and the adult wing is very short (Fig. 18): Curculionidae: *Premnotrypes solani* Pierce (Septopiinae, Premotrypini). 4—The pupal wing sheath is very short, and the adult wing is absent (Fig. 19): Curculionidae: *Pseudocneo-*



Figs. 15-20. Diagrammatic scheme of pupal wing sheaths of beetles, showing length of meso- and metathoracic adult wings and pupal sheaths; mesothoracic wings and sheaths in all cases; metathoracic wings and sheaths. 15. Adult long, pupa long. 16. Adult short, pupa long. 17. Adult short, pupa short. 18. Adult very short, pupa short. 19. Adult absent, pupa very short. 20. Adult absent, pupa absent.

hinus bifasciatus Roelofs (Eremninae, Cyphicerini); Salpingidae: *Aegialites alifornicus* (Motsch.) (Aegialitinae). 5—The pupal wing sheath is absent, and the adult wing is absent (Fig. 20); Curculionidae: *Brachycerus albidentatus* Gyll. (Brachycerinae, Brachycerini). Again, the sample is small, but some speculations on the occurrence of short or absent pupal wing sheaths are possible. In the Ptinidae described by Smith (1964) and in the Tenebrionidae and many of the other groups described by me, the short or absent pupal wing sheath occurs in those subfamilies or tribes in which brachyptery or winglessness is very widespread or total, as in the Gibbinae of the Ptinidae and in the Eleodini and Asidini of the Tenebrionidae. On the other hand, the long pupal wing sheath and brachyptery occur in those subfamilies or tribes in which brachyptery is infrequent, such as the Tenebrionini (*Centronopus*) and Meracanthini of the Tenebrionidae and the Carabini of the Carabidae.

Thus, if the adult beetle is brachypterous or wingless, one might predict from the length of the pupal wing sheath the approximate frequency of brachyptery or winglessness in the group to which the species belongs. More succinctly, in the case of wingless adults, a short or absent wing sheath indicates widespread winglessness in the higher group, such as tribe or subfamily, and a long pupal sheath indicates occasional winglessness. Briefly, in a brachypterous or apterous species the length of the pupal wing sheath is correlated with the frequency of winglessness within the higher taxa.

How does this phenomenon exhibit itself, if at all, in other kinds of winglessness? In beetles the tribe Necydalini of the Cerambycidae is a good starting point; adults of this tribe, like those of the Staphylinidae, have the elytra very short and the wings long. The pupa of *Ulochaetes leoninus*

LeConte has short elytral sheaths. This is not surprising, for the adult characteristic of short elytra is found throughout the tribe.

Intraspecific wing polymorphism was considered; I had only two kinds before me. The first concerns the caste system of ants, wherein most species have winged adult sexual forms and completely wingless adult workers. Pupae of both castes of *Camponotus conspicuus* (F. Smith) (Formicidae) were examined; the sexual form had two pairs of fully developed wing sheaths and the worker had absolutely no wing sheaths. This was to be expected because this kind of winglessness is widespread in ants. The second type concerns both sexual and temporal wing polymorphism. In the caddisfly *Dolophilodes distinctus* (Walker) (Philopotamidae) females that emerge in winter and spring are almost wingless, having both pairs of wings very small or atrophied. Females in other parts of the year, like males throughout the year, are fully winged. The pupae of winter and spring females have both pairs of wing sheaths almost as long as those of fully winged forms; inside these wing sheaths can be seen the very small adult wings. This condition in the pupa is as expected; temporal adult polymorphism, evidently an exception to the rule, has not greatly altered the pupal wing sheaths.

One might reason that a species having a brachypterous adult and a pupa with short wing sheaths is more efficient than a species having a brachypterous adult and a pupa with long wing sheaths. The development of a long wing in the pupa and then its subsequent degeneration into a short wing seems to be inefficient. The extra energy needed to form the unnecessary long wing and long sheath is wasted. It therefore seems obvious that selection would favor short pupal wing sheaths in a brachypterous species. If a taxon had evolved from the fully winged adult condition to the brachypterous or wingless condition far in the past, it would have had time to eliminate the development-degeneration phase of the adult wing in the pupal stage and to eliminate the long pupal sheath. If, on the other hand, a taxon had evolved from the fully winged condition to the brachypterous or wingless condition rather recently, it would not have had time to eliminate the development-degeneration phase of the adult wing in the pupal stage and would retain the long pupal sheath.

The above is only a preliminary investigation. Many other forms of winglessness in the Holometabola should be studied. Perhaps such studies could indicate whether or not a wingless condition was developed recently or far in the past. Other reduced or absent appendages or structures in insects should be observed in the pupal stage. The four-footed butterflies (Nymphalidae) come to mind; the prothoracic legs of the adult are much reduced. I'm sure many other possible fields of investigation could be suggested by other systematists and morphologists. In addition, we need to know the

effect on the pupa of genetic manipulation, such as that done on *Drosophila* and *Tribolium*. Finally, it follows that an investigation into the genetic control of pupal wing sheath and adult wing development is needed; is it governed by a single gene working in a simple Mendelian fashion, or how?

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LITERATURE CITED

- Craighead, F. C. 1950. Insect enemies of eastern forests. U.S. Dept. Agric. Misc. Publ. No. 657:1-679.
- Daggy, T. 1947. Notes on the ecology and taxonomy of certain pupae of the family Tenebrionidae (Coleoptera). Proc. Indiana Acad. Sci. 56:253-260.
- St. George, R. A. 1924. Studies on the larvae of North American beetles of the subfamily Tenebrioninae with a description of the larva and pupa of *Merinus laevis* (Olivier). Proc. U.S. Natl. Mus. 65:1-22.
- Smith, D. S. 1964. The structure and development of flightless Coleoptera: A light and electron microscopic study of the wings, thoracic exoskeleton and rudimentary flight musculature. J. Morphol. 114:107-183.
- Spilman, T. J. 1962. The New World genus *Centronopus*, with new generic synonymy and a new species (Coleoptera: Tenebrionidae). Trans. Am. Entomol. Soc. 88:1-19.
- Waddington, C. H. 1942. The development of rudimentary wings in *Ptinus tectus* Boield. (Coleoptera: Family Ptinidae). Proc. Zool. Soc. London, 112, Ser. A:13-20.